EGGSHELL THICKNESS AND ITS VARIATION IN THE CEDAR WAXWING

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Much recent literature has dealt with the interrelations of certain chlorinated hydrocarbons to reproductive failure and declining populations in various birds. Ratcliffe (1970) has summarized these interrelations which are mediated largely through changes in eggshell thickness. Despite the importance of eggshell thickness, general analyses of the factors other than certain pesticides that might affect it are scarce, save in the chicken (*Gallus gallus*) where economic considerations have prompted many studies (see Romanoff and Romanoff, 1949). Furthermore, data on eggshell thickness in songbirds are almost totally lacking, even though the latter constitute the majority of living bird species. This study analyzes the various factors which might reasonably be thought to be related to the eggshell thickness of a bird in nature. I have utilized eggs of the Cedar Waxwing (*Bombycilla cedrorum*), an abundant Nearctic passerine.

METHODS

Eggs were collected in 1968 and 1969 in Cheboygan and Emmet Counties, Michigan and one randomly chosen egg was measured from each nest. Shell thickness, with the membranes, was measured one-third of the way down from the blunt end of each egg, using a specially adapted Starrett No. 1010 M micrometer. Although this micrometer is graduated in units of 0.01 mm, readings were estimated to 0.001 mm. Blus (1970) and Kreitzer (1971) apparently also followed this procedure. Accordingly, all statistical tests were performed with readings in 0.001 mm. However, all of these statistical tests have also been performed with the data rounded off to 0.01 mm and the results are only slightly changed from those reported in this paper. (Comparison 2 of Table 1 provides the only statistical test which is no longer significant when the readings are rounded off to 0.01 mm.)

RESULTS AND DISCUSSION

Natural variation.—The data were divided on the basis of factors which might relate to shell thickness. Mean eggshell thickness was 4.2 per cent greater in eggs from three-egg clutches than in eggs from four- and five-egg clutches, with the difference significant at $P < 0.05$ (comparison 1, Table 1). A possible inference of this result is that the availability of material for eggshell formation may act as a limiting factor for clutch size. Although Lack (1968) made a comprehensive review of the relations of ecological factors to egg characteristics, the possible limiting role of material for shell formation was not considered. Another, although not necessarily mutually exclusive, explanation of shell thickness dependent on clutch size rests on work with

Table 1

Factors Related to Eggshell Thickness in the Cedar Waxwing

	Entire sample	All eggs with no development	Clutches of less than four eggs		Four and five egg clutches	
			Eggs with no development	Eggs with development	Eggs with no development	Eggs with development
Recent eggs (1968–69)						
Median (mm)	0.091	0.092**	0.093*†	0.087†	0.091*‡	0.086‡
(N)	(68)	(52)	(15)	(2)	(35)	(14)
Mean (mm)	0.091	0.092	0.095	0.087	0.091	0.087
Old eggs (1871–1912)						
Median (mm)	0.095**					
(N)	(22)					
Mean (mm)	0.095					

All the vital data could not be acquired for a few eggs. This explains the small changes in certain sample sizes when tabulated under different headings or in Table 1 versus Table 2.

* 1. Probability for difference between these two samples is <0.05 (two-tailed Mann-Whitney U Test; Siegel, 1956).

† 2. $P < 0.01$ (Randomization test for two independent samples; Siegel, 1956).

‡ 3. $P < 0.02$ (Mann-Whitney U Test).

** 4. $0.05 < P < 0.06$ (Mann-Whitney U Test).

the chicken. Within a set of eggs, shell thickness generally decreases with each successive egg, except for the last one (and the penultimate one as well in sets of six or more) (Romanoff and Romanoff, 1949; Wilhelm, 1940; Berg, 1945). The first and last eggs usually have similar shell thicknesses. A similar trend has been found in the Japanese Quail (*Coturnix coturnix*) (Bitman et al., 1969). If this type of trend occurs in songbirds, it could explain the observed relation between clutch size and shell thickness reported here for the Cedar Waxwing. Sixty-seven per cent of the eggs in clutches of three would have thick shells, but the comparable percentages for clutches of four and five would be only 50 and 40 respectively. The occurrence of this trend in songbirds would necessitate the use of nonparametric statistics, the type applied in this paper, because the frequency distributions for shell thicknesses of eggs from different-sized clutches would have different shapes.

Eggs with embryos had significantly thinner shells than ones with no development, as is shown by two independent tests (comparisons 2 and 3, Table 1). To determine whether shell thinning occurs throughout much or all of incubation, the ideal measure of incubation stage would be the number of days each egg was incubated before it was collected. However, this is difficult to determine, especially for species like the Cedar Waxwing which

TABLE 2

EGGSHELL THICKNESS AND DEGREE OF DEVELOPMENT OF EMBRYO (AS INDICATED BY ITS EYE DIAMETER) IN CLUTCHES OF FOUR AND FIVE EGGS

Diameter of embryo's eye, mm	Eggshell thickness, mm
1.6	0.087
1.9	0.090
2.2	0.089
3.0	0.084
3.0	0.103
3.6	0.091
4.1	0.090
4.2	0.081
4.3	0.095
5.0	0.082
5.1	0.073
5.4	0.080
5.5	0.079

Probability for above association is <0.025 (Kendall rank correlation, $\tau = -0.416$; Siegel, 1956).

normally begin incubating before the clutch is completed (Putnam, 1949; pers. obs.). Thus, it was decided that some easily measured attribute of the embryo, such as eye diameter, provides the most reliable measure of the amount of incubation and development. There is a significant association ($P < 0.025$) between the degree of embryonic development (as indicated by eye diameter) and shell thickness (Table 2), suggesting that thinning occurs throughout much or all of incubation. The thinning was probably due to withdrawal of calcium from the shell by the embryos. About 80 per cent of the calcium in the hatching chick of the domestic fowl is derived from the shell (Simkiss, 1961) and this withdrawn calcium amounts to about 5 per cent of the total shell calcium (Simkiss, 1967).

Seven eggs from the four- and five-egg clutches with no development (Table 1) had undergone incubation as indicated by their contents which consisted of slightly to strongly malodorous yolk and albumen. The average shell thickness of these eggs was close to that for the remaining 28 eggs in the subsample (0.092 mm and 0.091 mm, respectively), thus substantiating the interpretation that the shell thinning during incubation is due to the metabolism of the embryo and not to some ageing or deterioration process in the egg. Previous studies of birds in nature have not shown a definite relationship between shell thickness and embryonic development, although such a relationship is suggested by data for the Brown Pelican (*Pelecanus occidentalis*) (Anderson and Hickey, 1970). However, Vanderstoep and Richards (1970) have shown that shell thickness in the chicken decreases significantly between the tenth and eighteenth days of incubation.

Additional analyses done on the 1968–69 sample of waxwing eggs failed to detect correlations between shell thickness and the following: egg length, width, or volume and date or year of laying. Although longer eggs tended to have thinner shells, the association was not statistically significant ($P > 0.05$) with the Kendall rank correlation coefficient; Siegel, 1956).

It is apparent from the above analyses that the determinants of eggshell thickness in nature may be quite complex, with little studied ecological and physiological factors playing significant roles. Indeed, under laboratory conditions many factors have been found to affect shell thickness in the domestic fowl (Romanoff and Romanoff, 1949). The possibility exists that some factors could bias results in studies intended to deal primarily with the relation of shell thickness to certain pesticides. A problem of this type occurred in this study. Waxwing eggs from orchards on farms had a significantly greater incidence of sterility and/or embryonic death than eggs layed away from farms (Rothstein, in press). Direct proof was lacking, but the difference seemed to be most likely due to pesticides, and statistical analysis demonstrated that the farm eggs had significantly thinner shells. Further analysis, however, showed the farm sample to have a disproportionate number of incubated eggs (because collecting was done later on the farms than in the other study areas). Eggs with no development from each habitat type were then found to have almost identical shell thicknesses.

Possible "unnatural" variation.—Several nonpasserines and two large passerines have undergone statistically significant shell thinning since the use of DDT began (Ratcliffe, 1970), but this aspect has not been investigated in what are perhaps the most ecologically important of all birds, moderate or small-sized passerines. To determine whether the shells of Cedar Waxwing eggs have also become thinner, a series of pre-1920 eggs was measured. These eggs are in the U.S. National Museum and were collected in various parts of the waxwing's range. The data (comparison 4, Table 1) strongly suggest that current waxwing eggs have thinner shells than older ones. The degree of thinning (3.2 per cent) is probably not severe enough to have a significant effect on the population size of the Cedar Waxwing. But, incomplete records made it impossible to determine the incubation status of all of the old eggs, and some heavily incubated eggs may be included in the sample. Thus, the shell thicknesses of the old eggs may be biased by being too low whereas in the sample for the recent eggs, all the eggs with development have been excluded (comparison 4, Table 1). Therefore, the degree of thinning may be greater than is indicated by the comparison in Table 1. Furthermore, even a slight degree of thinning may have a deleterious effect on individual reproductive output, since the shell thickness previously extant was presumably better adapted than the possibly unnaturally thinned one reported here.

Based on the available evidence it would be merely speculative to suggest a causal relationship between chlorinated hydrocarbons and the probable shell thinning in waxwing eggs reported here. However, given the widespread nature of this type of causal relationship there is a possibility of its existence in the waxwing and in moderate or small-sized passerines in general and additional studies of eggshell thickness in such birds would be highly desirable.

SUMMARY

Eggshell thickness in the Cedar Waxwing was analyzed in relation to various factors and the existence of important natural variation was demonstrated. Eggs from small clutches have thicker shells than eggs from large clutches. Embryonic development results in a thinning of the shell. Five other factors failed to significantly correlate with shell thickness. Recent waxwing eggs appear to have slightly (3.2 per cent) thinner shells than eggs collected before 1920. The possible significance of these findings to clutch size determination and other factors as well as to pesticide studies is discussed.

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NEW LIFE MEMBER

Mr. Henry Bell, 3rd has recently become a Life Member of The Wilson Ornithological Society. Mr. Bell lives in Chevy Chase, Maryland and is a geologist with the U.S. Geological Survey. He holds a degree from the University of South Carolina and has also attended the University of Pennsylvania, Pennsylvania State University, and the University of North Carolina. His interests in birds are of long standing. He is a Fellow of the Geological Society of America and a member of the AOU and the Maryland Ornithological Society. Along with bird study he counts woodworking and boating as his hobbies. Mr. Bell is married with no children.